Territorial behavior of *Favonius taxila* (Lycaenidae): territory size and persistency

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Abstract: Territorial behavior of the hairstreak, *Favonius taxila* Bremer 1861, was investigated in Aomori Prefecture, Japan. Males were active in the morning hours, during which they showed territorial behavior. Territorial males persistently perched on almost the same leaf or a shoot and occasionally flew around a limited area, here referred to as inspection area. When another male intruded into this area, the resident and the intruder engaged in a circling flight. The flight occasionally strayed to outside of the inspection area, where it was terminated. The resident returned to his territory in most cases, but in a few cases, exchange of the territory owner occurred. In one case, a single butterfly occupied his territory throughout the observation period of 5 days, whereas in another, several times of exchanges occurred.

Key words: circling flight, intra-specific competition, residency, territory.

Introduction

For male mate-locating behavior of butterflies, Scott (1974) proposed three types: perching, patrolling and using pheromones. He stated that territoriality was absent or rare in butterflies. Recent investigations, however, revealed territorial behavior in many species, that perform perching behavior belonging to the families Nymphalidae (Watanabe 1977, 2002; Bitzer & Shaw 1980, 1983; Alcock 1985; Benson et al. 1989; Rosenberg & Enquist 1991; Lederhouse et al. 1992; Rutowski 1992; Kemp 2001), Papilionidae (Lederhouse 1982), Satyridae (Davies 1978; Knapton 1985), and Lycaenidae (Alcock 1983; Cordero & Soberón 1990; Fischer & Fiedler 2001). Rutowski (1991) cautioned that researchers should not confuse perching behavior with territoriality. Perching simply indicates staying in a specific area, whereas territorial behavior indicates a defense of a specific area.

According to anecdotal notes in a butterfly encyclopedia (Fukuda et al. 1984), some hairstreak species belonging to the tribe Theclini (Family Lycaenidae) show territorial behavior, occasionally comprising co-rotating flights between a resident and an intruder (Sibatani 1989). Such flights may last for more than 20 minutes in *Chrysozephyrus smaragdinus* Bremer 1861 (Fujii 1982). While other hairstreak species belonging to Theclini do not show territorial behavior, but show patrolling behavior for mating (Fukuda et al. 1984). Another characteristic feature of Theclini is that some species show conspicuous sexual dichromatism on their wings, whereas others do not. Therefore, they are ideal subject to study intra and inter- sexual selection. However, few systematic investigations have been made on behavior of butterflies of this group (but see Sibatani 1992). Their arboreal habits and relatively short activity period as adults (about a month) render field observations and experiments difficult.

To obtain systematic knowledge of their behaviour, we performed an observational study of a Thecline species, *Favonius taxila* Bremer 1861, at the foothills of Mt. Iwaki in Aomori Prefecture, where butterflies can be observed in close proximity to observers. Sibatani (1989) described males of *F. taxila* as showing the most conspicuous territorial behavior amoung species of *Favonius*. This paper reports activity time, territory size, occurrence of circling flights, and persistency of territory occupancy in this species.

Study species, Study site and Methods

Males of *Favonius taxila* have brilliant green dorsal wing surfaces due to interference of light. By contrast females are mostly black or dark brown. Forewing length is approximately 20 mm. This species inhabits deciduous forests in Hokkaido and Honshu, Japan, and is also distributed in northeastern China, the Amur region and Sakhalin in Russia, and the Korean peninsula

(Fukuda et al. 1984, Gorbunov 2001). Adults emerge once a year, mainly in July.

The field study was carried out near Dake Spa at the southern foothills of Mt. Iwaki in Aomori Prefecture (140° 20'E, 40° 40'N) from 13 to 19 July 1998 and from 18 to 23 July 2000. The study area was along a narrow path in deciduous forest. The main observation site was in grass and bushland (ca. 15 m x 30 m, Fig. 1) comprised of lower plants such as *Weigela hortensis* and ferns of 2 m height or less. The site was surrounded by forest containing *Quercus mongolica* trees 10 to 15 m tall (Fig. 1), the larval food plant of *F. taxila*. Butterflies appeared at the observation site, flying down to the grass and bush land and to the edge of the forests during a particular time of a day. We refer to this time period as activity time.

To obtain data of activity time, the main observation site was surveyed for flying or perching butterflies by slowly walking along the path every 5 to 60 min from 6:00 to 18:00 on days with sunny weather. Air temperature was measured with a thermometer hung in the shade on a tree at 1 m height.

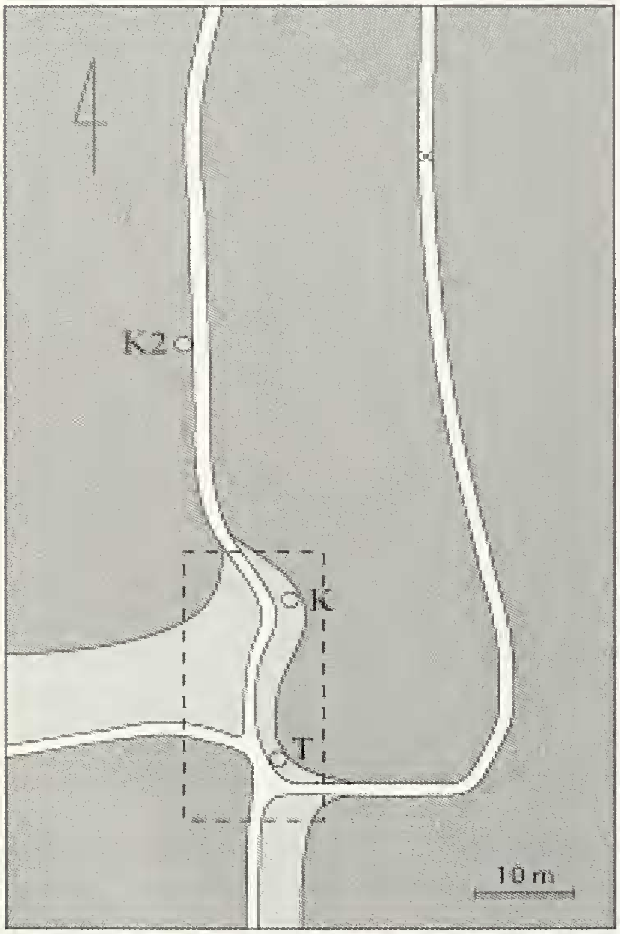


Fig. 1. A map of the study area. Dark gray: tall trees, Light gray: lower plants, White: bare ground (path) The dashed lined square is the main observation site. K, K2, and T are locations of the mainly observed territories.

For the investigation of territorial behavior, males were captured and marked with a black or pink felt-tip pen (Mitsubishi™) along the edges of the ventral surface of the fore- and/or hind-wings of both left and right sides (Fig. 2). A total of 29 and 22 individuals were marked in 1998 and 2000, respectively.

During the activity time, a male who had occupied a territory as 'resident' typically perched on a fixed point, such as the tip of a shoot or twig of a tree, and occasionally and spontaneously flew around the perch point without being approached by other individuals. These spontaneous flights covered a limited range, which is referred to hereafter as the 'inspection area'. Inspection areas of resident males were recorded when they were most active during a day.

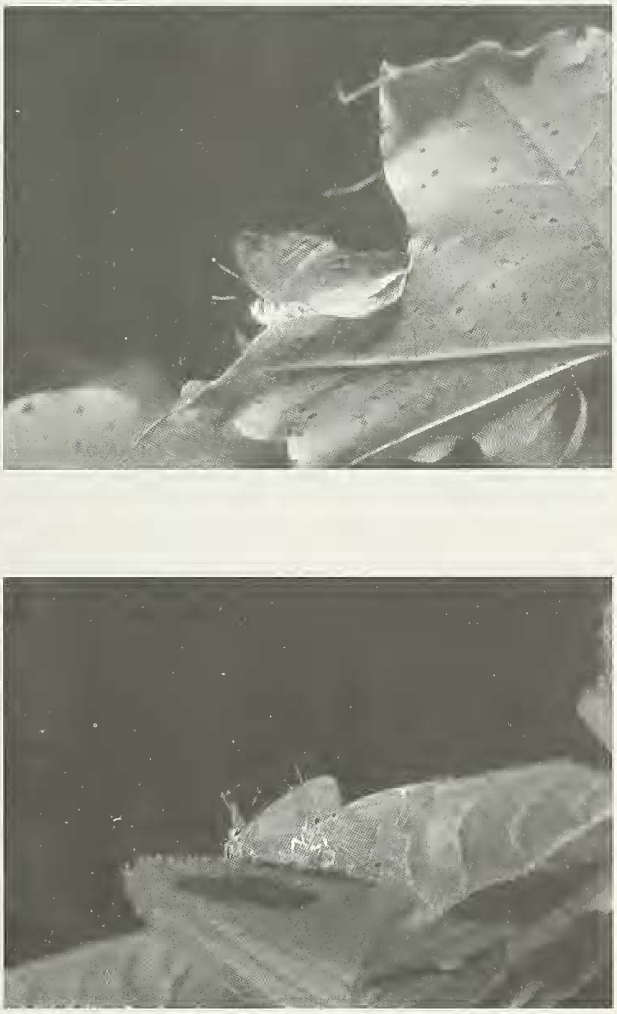
Residents reacted to approaching conspecific males with a particular flight: both individuals commenced with a rotation flight, which is traditionally called "manjidomoe" flight in Japanese (Fukuda et al. 1984). Other authors have termed this type of interaction spiral flight (Davies 1978), co-rotating flight (Sibatani 1989) or circling flight (Kemp 2001). Here we refer to it as circling flight. In *F. taxila*, two butterflies in circling flight circle in vertically separated planes (Fujii 1982).

The points where the circling flight was initiated and terminated, respectively, were plotted in a map. Initiation points were those at which the intruder was located when the resident started to rush towards him. These data were recorded when the butterflies were most active. To determine duration of territory occupation, residents of a territory were recorded every 15 minutes during activity time. This recording was made for 5 and 4 days respectively during 1998 and 2000.

Results

Activity time and behavior

The number of *F. taxila* males counted at the main observation site is shown in Fig. 3. The activity time ranged from 7:30 to 11:30 in 1998. In 2000, butterflies were already active at 7:00 and became inactive by 11:00. Thus, the activity time was slightly earlier in 2000 than in 1998. Air temperature was also different



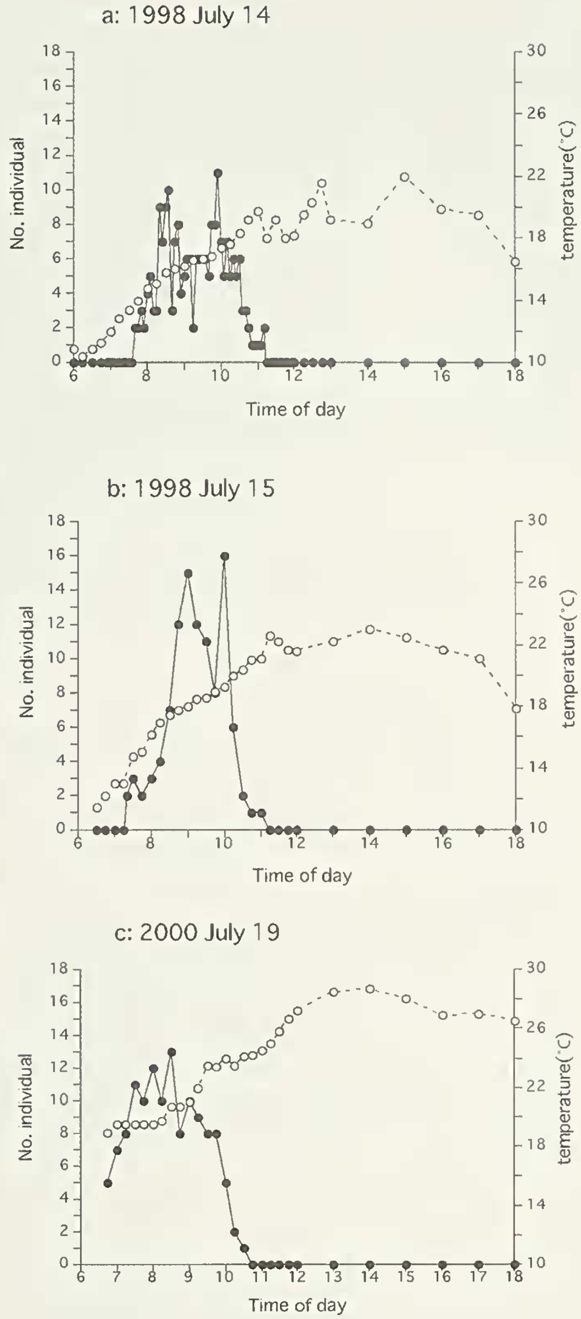


Fig.2a . A marked male exhibiting territorial activity, b: two males perching on the same leaf at the end of activity time.

Fig. 3. Daily activity of *Favonius. taxila*. The number of male *F. taxila* observed in the main observation site (solid circles) and air temperature (open circles) are shown.

between the two years: the air temperature at 7:00 was 12°C in 1998 and 20°C in 2000.

Prior to territorial activity, several butterflies were observed flying weakly around the canopy at approximately 10 m height and then coming down to lower places such as on the grass or bush surface where they basked with their wings opened. Thereafter, they initiated territorial activity. At the beginning, they seemed relatively insensitive to intruders, and occasionally disappeared from their territory for a while. Soon, they became responsive to intruders and persisted to their territory. During their territorial activity, they perched, with their wings opened, on a shoot or a twig extending from the bush (Fig. 2a). As the end of activity time approached, males became relatively less active again; they frequently perched with their wings closed and became insensitive to intrusion of other males. On a few occasions, two butterflies were found simultaneously perching on the same single leaf within the territory of one of them (Fig. 2b). At the end of activity time, butterflies were observed to fly up to high places, or could be found imbibing water on the ground.

Females were rarely seen during activity time, but near the end of the activity time, a few females were observed on the grass near or in a male's territory. However, mating behavior was not observed. At the main observation site, a closely related species, *Favonius jezoensis* Matsumura 1915, was found active and showed territorial behavior in the afternoon.

Inspection area

In 2000 the vegetation around the main observation site had largely been changed by bush cutting, and grasses were shorter than in 1998. The inspection area was approximately 33 m^2 for territory T by male No.8 in 1998, and approximately 60 m^2 by male No.9 and 32 m^2 by male J for territory K in 1998 and 2000, respectively (Fig. 4).

Circling flight

During activity time, the territory resident frequently interacted with intruding insects. In almost every case, the intruding insect was a conspecific male. The locations of the intruder when the resident started to rush toward him are shown in Fig. 4. Almost all points were located within the inspection area. After the encounter, the two individuals performed a circling flight in a small circle for a period of a few seconds to several minutes. In a circling flight, the pair strayed apart, and occasionally moved out of the inspection area.

After almost every circling flight, the resident was confirmed to have returned to his territory, and the intruder flew away. The male returning after the interaction was defined as the winner of this interaction. There were so many circling flights that we were unable to record all of them. Therefore, we recorded the number of circling flight during specific periods. During the most active time from 9:02 to 9:49 on 14 July 1998, the resident of territory K (male No.9) engaged in 70 circling flights and "won" all of them. The resident in territory T (male No.8) also "won" all 36 circling flights observed from 9:00 to 9:30 on 16 July 1998.

Maintenance of territory

The residents of territories T and K on consecutive days are shown in Fig. 5. Territory T was occupied by a single individual, No.8, throughout the observation period from 15 to 19 July 1998. On the other hand, in territory K in 1998, the owner changed at least from No.9 through No.2 to No.3 in 5 days. Individual No.9 disappeared from territory K on July 15, but was later found to hold a new territory in another site approximately 30 m north from the original territory (K2 in Fig.1) on 16 July. In 2000, 5 individuals alternately occupied territory K.

The number of consecutive days that a resident was observed in a territory is defined as his residence duration (here, a resident is defined as the male that occupied the territories for more than two consecutive observation times). Mean residence duration was 1.6 days ± 1.3days (N=10). It should be noted that during an early hours of the activity time on a day, a foreign individual occasionally occupied the territory, but was soon expelled by the habitual resident who came to the territory later (Fig. 6).

On 16 July in 1998, the resident of the territory T (No.8) was found imbibing water on the ground approximately 70 m from his territory beyond the canopy (cross in Fig.1) after the activity time. On the subsequent day, this individual was again found in the same territory as the previous day, suggesting that butterflies have some kind of spatial memory about the location of their territories.within a limited area.

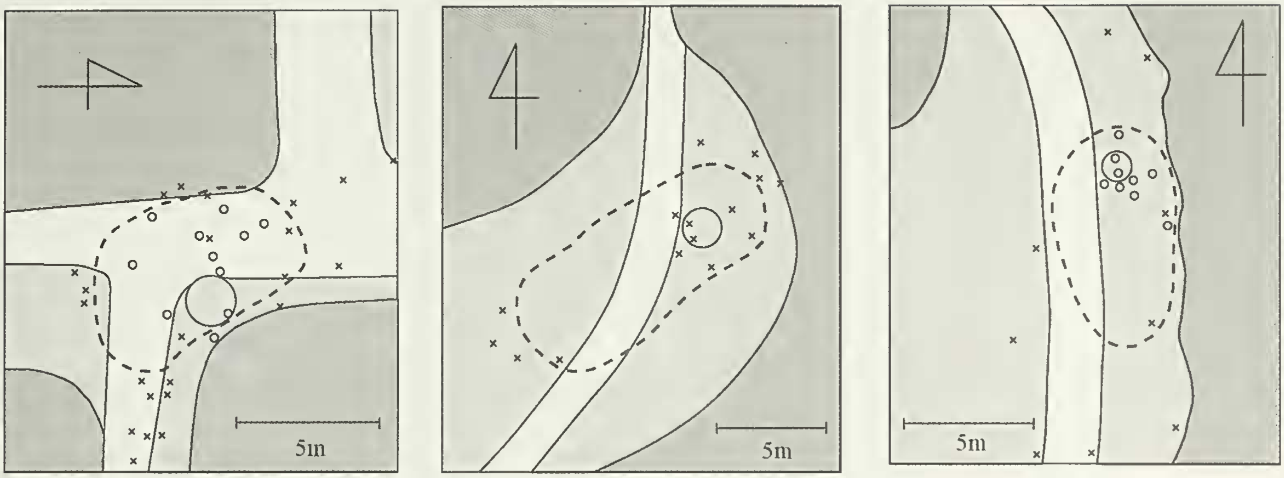


Fig.4 Map of territory structure of *Favonius. taxila*. Dark gray: tall trees, Light gray: lower plants, White: bare ground (path), dashed lines: inspection area, circles: initiation points of circling flight, crosses: termination points of circling flight, Large circles: the plant in a territory where resident often perched. a; the territory T in 1998, b; the territory K in 1998, c; the territory K in 2000. The locations of territories (K and T) are shown in Fig.1. Fig.4b lacks circles because we did not recorded the initiation points.

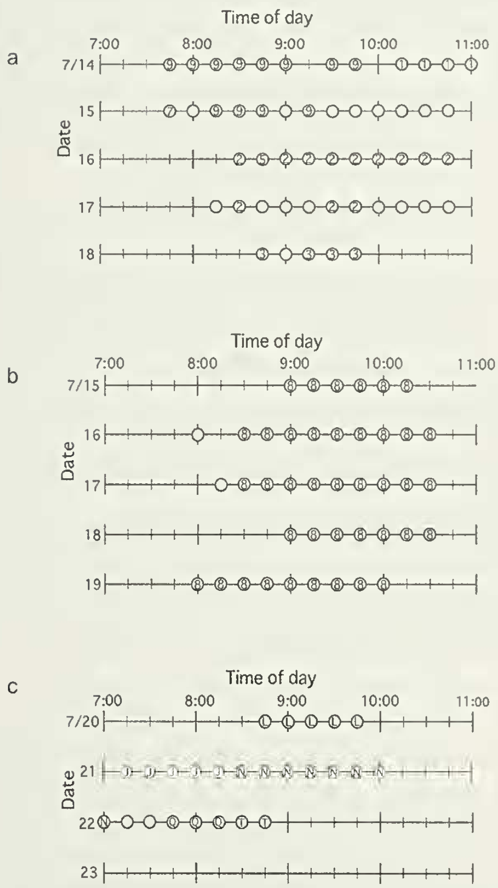


Fig.5 The resident of the territory T in 1998 (b), and of the territory K in 1998 (a) and in 2000 (c) on consequent days. The individual that occupied the territory at each time is indicated by the identification character. Open circles represent unmarked individuals or individuals we could not identify. In the territory K on 23 July 2000, no males were observed because of rain.

Discussion

The activity time of *F. taxila* was limited to morning hours. This result coincides well with previous observations (Fukuda et al. 1984). One possible proximal factor that determines the activity time is air temperature, as suggested by later appearance in 1998, a cooler year, than in 2000. However, the morning activity may not be simply determined by air temperature because butterflies were not active in the afternoon even though temperatures in the evening did not largely differ from those during most of the active time in the morning. It appears likely that gross activity time is determined by some internal timing mechanism, e.g. a "physiological clock" (e.g. Sørensen & Loeschcke 2002).

What are ultimate causes of the limited morning activity? At the present field site, a closely related species, *Favonius jezoensis* also occurs. This species, which is very similar in appearance to *F. taxila*, appeared and showed territorial activity in the afternoon. Thus, temporal segregation of the same space may be achieved between these species. Sibatani (1992) described that males of sympatric species of *Favonius* are partitioned with respect to their flying time during their territorial activity. He hypothesized that temporal segregation of flying time would exist in this genus. To test this assumption, it is necessary to examine the activity time of both species in the habitats where only one of them exists.

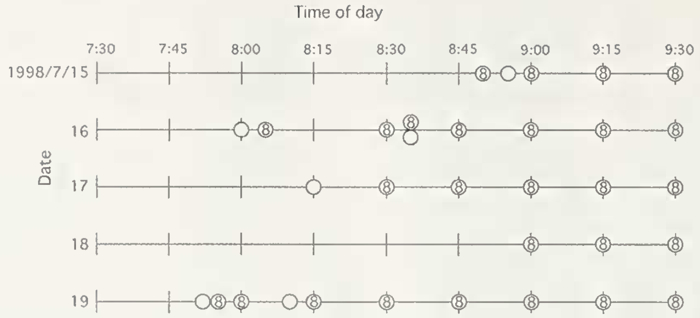


Fig.6 Details of the shift of individuals that occupied the territory T in 1998 at the beginning of the activity time. Open circles indicate unmarked individuals. Two circles at 8:35 on 16 July indicate that the two individuals competed seriously for the territory.

It has been generally claimed that the resident of a given space is superior to an intruder in a territorial contest, a phenomenon called "effect of prior residence" (Ito et al. 1992). In butterflies, the "effect" has been observed in many species (reviewed in Kemp & Wiklund 2001). So, why do residents successfully defend their territories? According to the arbitrary asymmetry hypothesis, residents defeat intruders because competitors adopt a rule to fight seriously when one is the resident and to retreat when he is the intruder (Bourgeois strategy; Maynard Smith 1976). Davies (1978) showed that this strategy appears adopted in the speckled wood butterfly, *Pararge aegeria* Linnaeus 1758. However, Van Dyck et al. (1997) showed that wing color patterns, which correlate with thermal condition, play an important role in adult behavior. Recent work showed that in *Parage aegeria*, the male whose body temperature was artificially controlled at 33.8°C won the territorial contest with the male whose body temperature was controlled at 26.7°C (Stutt & Willmer 1998). These body temperatures correspond to those of butterflies whose ecological status were a sunspot resident (33.8 °C) and a patroller in the wood (26.7 °C). Is it true that resident win also in nature because he can regulate his body temperature in the territory? In *F. taxila*, this seems unlikely. At the beginning of the activity time of *F. taxila*, a foreign individual that came into the space earlier than habitual resident and temporary occupied the territory, was later expelled by the habitual resident who came to the place later (Fig.6). If resident wins because he can regulate his body temperature in his territory, the foreign individual (temporary resident) would defeat the habitual resident in that situation because he could regulate his body temperature in the territory while habitual resident could not. Thus residents win many contests one after another. If thermal conditioning plays a crucial role in conflict, residents could not win so frequjently in a short period (70 fights in 49 min or 36 fights in 30 min) because residents would lose body temperature by convective cooling during flight. This suggests that habitual residents have higher resource-holding potential (RHP: Parker 1974) for combat or else give higher value for the territory than intruders (Leimar & Enquist 1984). Note that RHP in butterflies' combat has not been yet clarified (Kemp & Wiklund 2001).

Territory residents showed spontaneous flight within a limited area. This behavior seems to provide inspection of the territory. Therefore we named this space inspection area. Similar behavior has been observed also in *Oeneis chryxus* (Knapton 1985) and in *Lycaena hippotho* (Fischer & Fiedler 2001). We define territory as a range of the inspection area. Ideally, the territory range should be determined by connecting the outermost points at which circling or fighting flights occurred. However our observations were too limited to provide this more precise data.

In the present study, the locations of the onset of circling flight were limited within the inspection area, whereas termination of these interactions frequently occurred outside this area. The situation also occurs with other butterfly species as *Oeneis chryxus* (Knapton 1985), *Lycaena hippothoe* (Fischer & Fiedler 2001), and *Polygonia c-aureum* (Watanabe 2002). The situation also appears different from observations with other animals: in mammals and birds aggressiveness frequently declines near the boundary of the territory (e.g. Matsubara 2003). In the case of butterflies, it appears usual that territories are not adjacent to each other, but neutral spaces are maintained among them (Knapton 1985). Chase or attack seem to continue into such neutral spaces.

Males of *F. taxila* showed territorial behavior and apparently do not use alternative strategies such as patrolling as has been observed in other butterflies (Davies 1978; Kemp 2001). Patrolling is a male mate-locating strategy for finding females while in flight without specific site fidelity. Our evidence leaves unclear whether territorial strategy is better for *F. taxila* than patrolling to acquire mates. We found few females that entered the territory. In a related territorial Thecline species, *Chrysozephyrus smaragdinus*, females were observed to enter a male's territory accompanying a chase flight or mating attempt by males, and, though rarely, to copulate with the territory male (Fukuda et al. 1984). Similar phenomena have been observed in other butterflies (Lederhouse 1982; Wickman 1985; Alcock 1985). In *Pararge aegeria*, females appeared in territories of males more frequently than at other sites (Davies 1978), and all four virgin females released and successfully observed copulated with territorial males, but not with non-territorial males (Wickman & Wiklund 1983). Further close observations of *F. taxila* are needed to clarify females' appearance and behavior in males' territories.

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